

Microarthropod Population Gradients and Aggregations in the Soil of a Mixed Temperate Deciduous Forest

by

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With 4 figures

ABSTRACT

Population gradients and aggregations of springtails and mites in the uppermost 5 cm of the soil of a mixed beech-oak-pine forest were studied. Definite gradients along axes between tree trunks could be detected, which often had opposite directionality for different microarthropod species. Within larger-scale aggregations, often measuring several metres of diameter, smaller aggregations were detected, especially in the *Cryptostigmata* (*Oribatei*) group. Other features of the forest, such as fungi and pathway structures, are discussed in terms of their significance to population aggregations and gradients.

INTRODUCTION

Soil systems contain some of the most species-rich communities in nature. Well-developed temperate woodland soils may contain up to a thousand species of soil animals alone, including several hundred species of mites and springtails (ANDERSON 1975).

Knowledge of the distribution pattern of soil microarthropods is an important prerequisite for many ecological studies such as energy flow analyses, population biology, or human impact studies on soil invertebrates. The distribution of microarthropods within a single soil has been examined by, e.g., HAARLOV & WEIS-FOGH (1953), EIT-MINAVICIUTE (1959), WOOD (1967), ANDERSON (1971), PANDE & BERTHET (1975), and MITCHELL (1978). According to these studies as well as our own (SCHENKER & STREIT

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1980), we know that microarthropod populations often occur in rather clumped dispersion patterns of different sizes and exhibit population gradients which are difficult to attribute to environmental factors.

The origin of the aggregated distribution patterns and gradients of microarthropod populations is not definitely clear. Some hypotheses, according to BERTHET (1964), are the following:

1. Eggs are generally laid in patches, and the animals remain near the hatching place. This might be a possible explanation for rather small-scale aggregations.
2. The animals are aggregated in places where they find the best microclimatic conditions, especially humidity.
3. The animals have marked feeding habits and are clumped where it is possible to satisfy these.
4. The animals are inherently gregarious.

It is still an unsolved problem, whether these clumps are distributed more or less randomly within the temperate deciduous forest or according to an as yet unknown regulating system. Correlations between clumps of Cryptostigmata (= Oribatei) mites and some abiotic factors such as moisture or nutrient content of the soil have sometimes been found (MITCHELL 1978, SCHENKER 1981). ANDERSON & HALL (1977) have found a strong positive correlation between mite species diversity and microhabitat diversity. But most correlations found so far between population densities and macroclimatic structures are weak and cannot contribute more than a small part to a model of the macrodistribution of mites and springtails in soils.

In the present study, we try to answer the following questions: How large are aggregation units of microarthropod populations in mixed deciduous forests? Are the aggregations rather weakly or unequivocally demonstrable? In order to get an answer to this problem, we correlated densities of microarthropod groups and single species to obvious forest structures, such as tree trunks. In a second step, we also correlated densities to environmental factors and tried to answer the second question: Are the distribution patterns found in the mixed deciduous forest explained to a large extent by environmental factors?

The present study is a preliminary report. A more detailed description is in preparation.

METHODS

a) Studying area

The forest under consideration was a mixed deciduous forest of the *Querco carpinetum* association, on a brown loess soil, approximately 6 km south of Basel (Bruderholz, 390 m above sea level, mean annual temperature 9.4° C, mean annual precipitation 842 mm). Pine trees had been introduced long ago, so that the most dominant tree species now are the beech (*Fagus sylvatica*), the oak (*Quercus robur*), and the pine tree (*Pinus sylvestris*).

Through the action of a freezing rain in the winter 1977/78 a great amount of wood (branches and whole trees) had fallen onto the ground and was removed by man during the following two winters. Together with cut trees, a large amount of wood, approximating the amount of many years' forest production, was removed in these two winters (1977/78 and 1978/79). Thus, when we started our sampling period, a relatively loose structure of the forest was encountered, the mean distance between trees

varied between about 4 and 15 metres. The ground vegetation was not very dense and consisted of a variety of plants typical for the *Querco carpinetum* of this region (cf. SCHENKER 1981). Many vehicle tracks had persisted and could in part be seen several years later. The study began in January 1979.

Within the forest, we looked for a situation where the three most abundant tree species were found at approximately equal intervals (about 12 metres), thus forming a triangle with no other tree within this triangle (with the exception of a newly cut beech stump). Samples were taken at approximately equal distances between the trees (0 m, 3 m, 6 m, 9 m, 12 m) and around the trees (at approximately 30, 50, 70, and 90 cm from the trunks).

b) Extraction of animal materials

Microarthropod samples were taken monthly for one year (January 1979 to February 1980). Samples were taken with a core sampler (BIERI *et al.* 1978a). Extraction of the arthropods was performed during a 6 days' extraction procedure in an altered version of the MACFADYEN extraction apparatus, as described in BIERI *et al.* (1978b). An individual sample had a diameter of 5.8 cm and a depth of 5 cm, so comprising a volume of 130 cm³. 69 to 96 core samples, all lying in the uppermost 20 cm layer, were taken. Only the top 5 cm core units were used for the data presented in this paper.

A rough separation of the main microarthropod groups (Collembola: Arthropleona and Symphypleona; Acari: Cryptostigmata, Mesostigmata, Prostigmata, Astigmata) was followed by determination of the species of some of the groups by specialists.

c) Mapping

Mapping of species abundances was performed by using the GEOMAP program (Dept. Geography, Univ. Waterloo, Ont., Canada), available through the University's computer centre.

d) Physical and chemical determinations

Physical and chemical determinations (especially soil temperature, solar radiation, humidity of the soil, pore volume, carbon content, nitrogen content, C/N value, Ca content, Na content, K content, cation exchange capacity, pH) were performed according to usual methods and taken from other cores than the ones that had been used for extraction of the microarthropods. Correlations to microarthropod numbers were calculated using non-parametric correlation coefficients (Kendall rank correlation coefficient and Spearman rank correlation coefficient).

RESULTS

Group and species densities of samples were measured at different distances from adult trunks of three tree species that were the most abundant in the forest under consideration. The following results exemplify results that will be described in more detail elsewhere:

At equal distances of approximately 3 metres between each combination of the three tree species, the densities of the different microarthropod groups were determined. The Cryptostigmata and the Collembola (consisting mainly of Arthropleona) groups

for June 1979 are plotted in Fig. 1. There was a clear minimum of both the Cryptostigmata and the Collembola between all the tree individuals, but around the oak, we found densities not higher than those found between the three tree specimens. This relationship persisted nearly for the whole year in the Cryptostigmata group, but was found only in the late spring/early summer samples in the Collembola group.

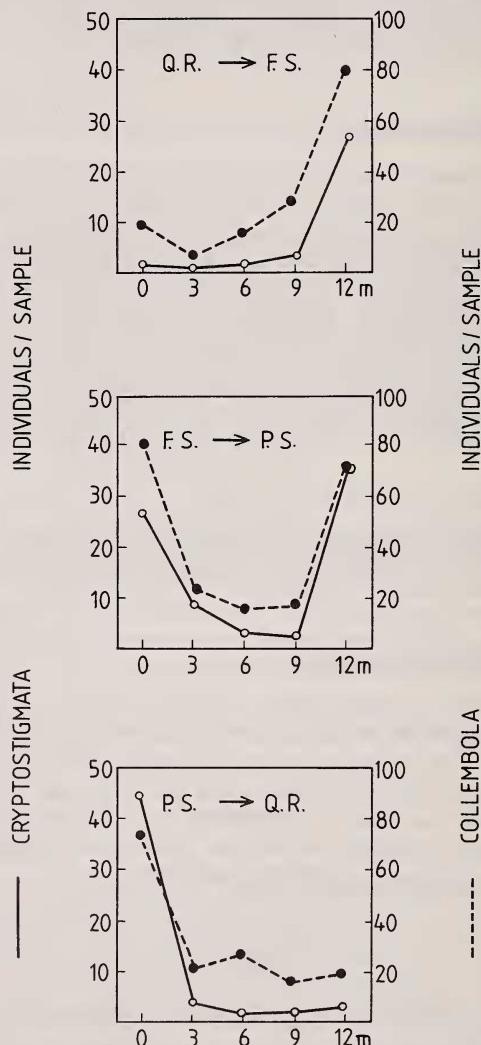


FIG. 1.

Group abundances between (a) oak (Q.R.) and beech (F.S.), (b) beech and pine (P.S.), and (c) pine and oak, as extracted in June 1979 from 130 cm³ samples of the uppermost 5 cm layers. Overall preferences to the beech and the pine locality are very obvious. At other dates of the year, and especially in other microarthropod groups, this pattern was often much less well developed.

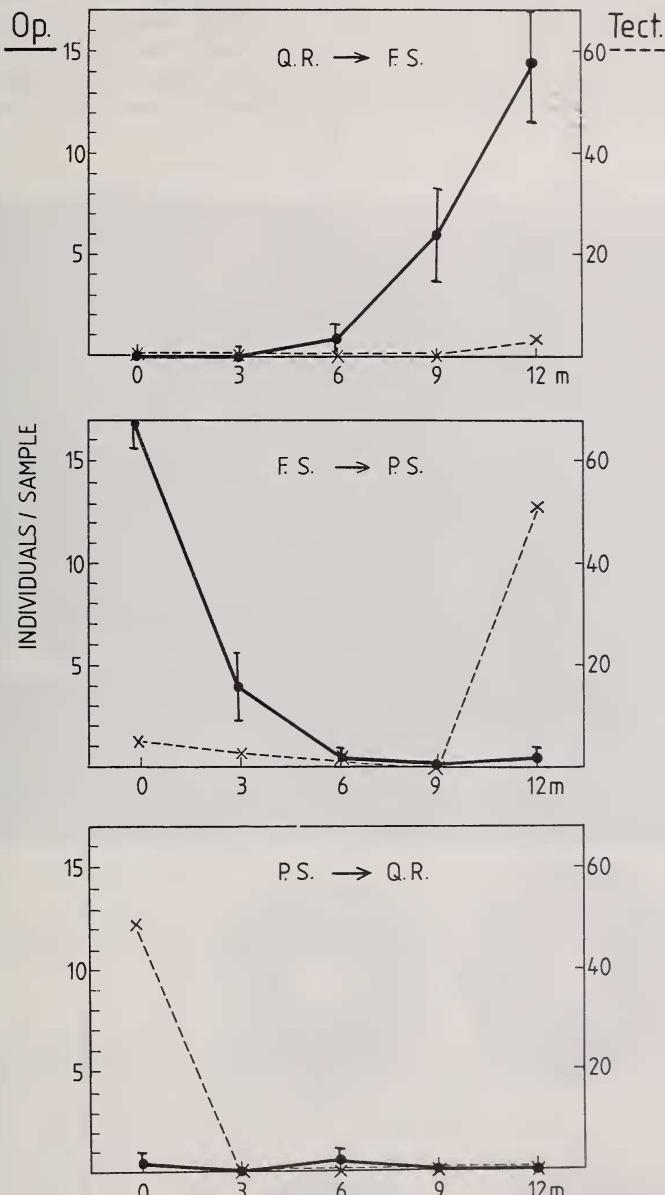


FIG. 2.

Densities of the Cryptostigmata species *Oppiella nova* OUD (Op.) and *Tectocephalus velatus* MICH (Tect.) between the same tree specimens as in Fig. 1. Values indicate numbers of adults and standard deviation per 130 cm^3 sample, as found in March 1979.

CRYPTOSSOMATA

ARTHROPODONA

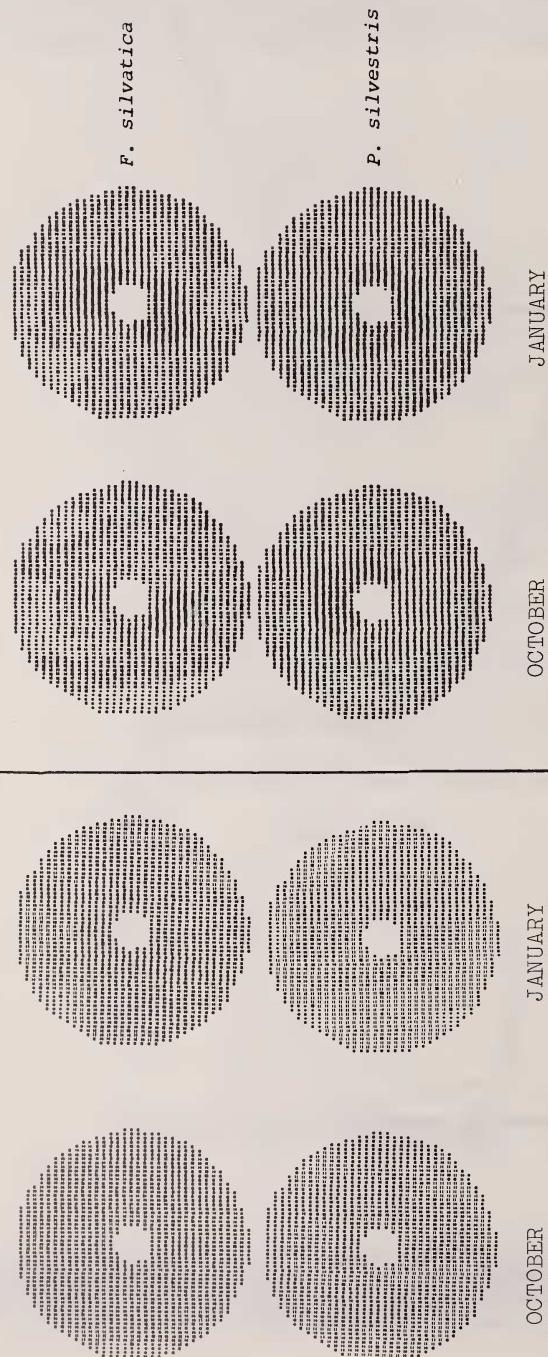


FIG. 3.

Densities of Arthropoda and Cryptostigmata around the beech (*F. sylvatica*) and the pine (*P. silvestris*). Scale 1:80. Small-scale aggregation patterns, beside the existence of the large gradients (Fig. 1), are detectable, especially in the Cryptostigmata group. Individuals per 130 cm^3 sample of the top 5 cm:

0-2;	2-6;	6-14;	14-30;	30-62;	62-126;	126-254;	254-510
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In comparative studies around other specimens of the same tree species, it was found that these tree-near aggregations are not the same around all the tree specimens of the respective tree species. Therefore, explanations for aggregations according to Fig. 1 cannot yet be definitely given in terms of the distance from a certain tree species.

In some cases, these overall densities in microarthropod groups are caused primarily by the numerical dominance of a single species. The density of just one important



FIG. 4a.

Photograph of the study area, indicating pathway, as taken in spring 1982.

species of the Cryptostigmata (*Oppiella nova* OUD.) was found to follow a gradient as presented in Fig. 2. The high density of *Oppiella nova* around the beech dominates the Cryptostigmata fauna there, as may be seen by comparison of Fig. 1 (Cryptostigmata lines) and Fig. 2. But *Oppiella nova* is very rare around the pine site as well as around the oak site. (This distribution pattern as revealed here by *Oppiella nova* in March 1979, was not so striking during the other seasons of the year). *Tectocephalus velatus* MIICH. on the other hand was rather abundant around the pine. By comparing Fig. 1 and 2, attention should be paid to the fact that Fig. 1 data represent June values, Fig. 2 March values.

Aggregation patterns in the two ecologically similar groups, the Arthropleona and the Cryptostigmata, differ. The difference in smaller scale distribution patterns in the close neighbourhood of the beech and pine trees is exemplified by the situation in October

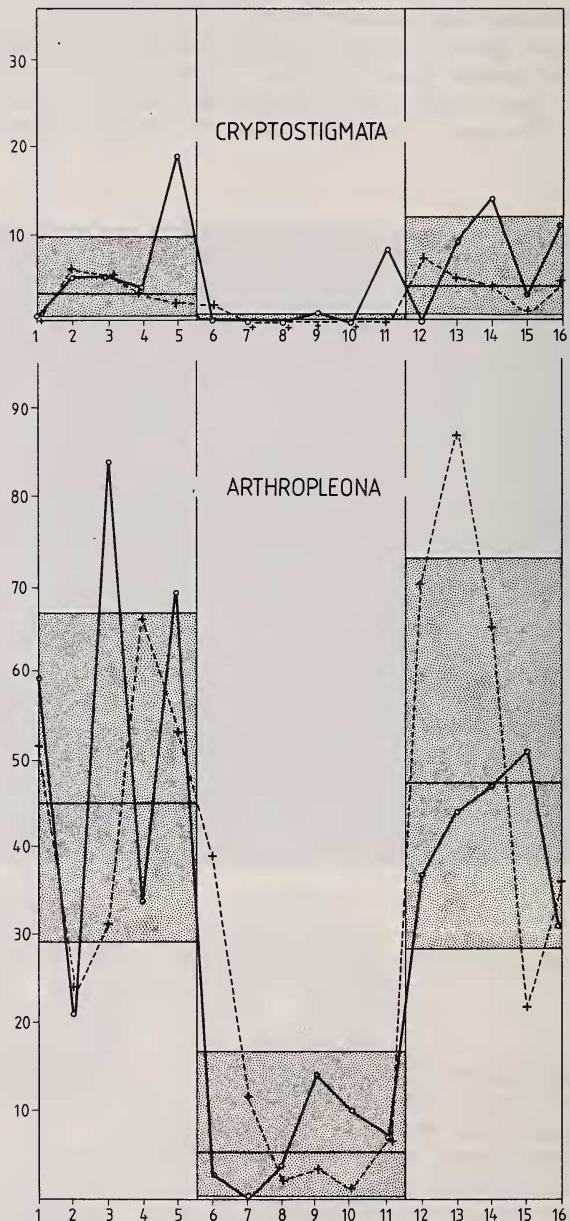


FIG. 4b.

Total numbers of Cryptostigmata mites and of Arthropleona, as found at two pathway transects within the study area in August 1981. Each sample of ca. 6 cm diameter was taken next to its neighbouring sample, except at the pathway borders (5/6 and 11/12 position), where a distance of about 6 cm was left between the two adjacent samples. Total distance of the transect therefore about 108 cm. Mean values of two transects and \pm one standard deviation (based on cubic roots) are indicated.

1979 and January 1980 (see the computer map in Fig. 3). The scale is approximately 80 times smaller than the original site. The Arthropleona group was more equally distributed than the Cryptostigmata group. The aggregated distribution pattern of the Cryptostigmata is much more strongly expressed.

The influence of fungal hyphae on microarthropod numbers was estimated by extracting core samples exactly below the fruiting bodies. It was expected that rather suitable feeding possibilities would be found in this small area of soil. Total numbers of the Cryptostigmata were not higher than elsewhere, those of the Arthropleona were somewhat higher on an average, and those of the Mesostigmata were significantly higher than at other sites.

During the period of 1980 approximately, people have begun to use a definite path which crossed through our study area. We determined abundances beside and directly in the pathway in August 1981. All microarthropod groups exhibited rather low figures of abundance (Arthropleona, Symphypleona, Cryptostigmata, Mesostigmata, Prostigmata). The only exception — consisting of relatively small individuals always arranged in small-scale aggregations — was found in the Astigmata group, which was found at about equal densities beside the pathway as well as in the pathway. The very sharp density gradients at the border between the pathway and the normal soil correlate with several factors, such as pore volume, humidity, or litter content on the surface (which was lowered through unintentioned removal of leaves by pedestrians). Besides the difference in total number, there is an obvious association difference, in that larger species, e.g. the Cryptostigmata species *Platynothrus peltifer* and *Phtiracarus laevigatus* (dry weight approximating 10-50 µg), are excluded from the pathway. Species still found in the pathway are primarily small-sized, such as *Opiella nova*, weighing 1-3 µg.

Pathways — either of human or of animal origin — could therefore represent interruption stretches for many populations of soil dwelling microarthropods (Fig. 4a + b).

DISCUSSION

According to ANDERSON (1977), soil animals are not organized in well defined communities. The centres and boundaries of species populations are scattered along macro-environmental gradients such that at any points on the gradient a species assemblage is found which is extremely difficult to associate with vegetation type or physico-chemical features of the habitat. This situation may be partially the result of failing to define the environmental variables at a scale which is meaningful to the animals and/or choosing the correct variables to describe the habitat.

It was therefore somewhat surprising that it could be stated in this study that aggregations and gradients of microarthropod populations in the mixed deciduous forest under consideration can be clearly established, if correlated to somewhat "arbitrary" and complex forest structures, such as tree species or human pathways.

It was found in this study, that the aggregations and gradients:

1. Are not purely arbitrarily distributed, but are correlated to some structures in the habitat. Important structure units are tree trunks. Abiotic factors, as hypothesized by MITCHELL (1978) and others may also be of importance. Selective influences of organic compounds released through the tree leaves or roots would be another possible factor, yet the leaf assemblages were not very different at the different sites.
2. There exist aggregations several meters in diameter, in which smaller aggregation units are scattered (Fig. 3). These small-scale aggregations correspond to those found

by us in a neighbouring forest and by a somewhat different method of sampling (SCHENKER & STREIT 1980). The large-scale aggregations are not delimited by a sharp boundary, but rather by a gradient, suggesting either the existence of a similar gradient of the regulating factor or the effect of some diffusion based outspread of the whole aggregation (cf. also STREIT & ROSER-HOSCH 1982). Trees are more important than fungi in this respect. The effects of herbaceous ground cover have not been tested. Human pathways seem to be a more or less pronounced boundary between adjacent aggregation sites.

3. Different taxonomic groups exhibited different distribution patterns: (a) The sluggish Cryptostigmata are found in rather well-established aggregations, (b) Collembola in less well established ones; (c) the often predatory and agile Mesostigmata exhibit more equal distribution patterns.
4. A purely deterministic explanation, basing population densities on measurable and macroenvironmental factors alone, does not seem to be possible. SCHENKER (1981) tested the influence of humidity, pore volume, pH, organic substances, carbon, nitrogen, C/N ratio, Ca, Na, K, and cation exchange capacity on the total number of Cryptostigmata as well as on the density of single species of this group. He only found a positive correlation between Cryptostigmata number and organic substance content (Kendall rank correlation coefficient = 0.222, Spearman rank correlation coefficient = 0.300). Another correlation was found between the density of *Bra-chychthonius berlesei* and the Na-concentration (Kendall correlation coefficient = 0.245). This may represent a causal relationship between the arthropods and mineral source, as postulated by CROMACK *et al.* (1977), but random correlations should not be completely excluded from having occurred in the analysis cited. Much stronger correlations are reported to have been found by ANDERSON & HALL (1977) in the analysis between micro-scale habitat structural complexity and mite species diversity. Based on all these facts, we would assume that macroaggregations possibly arise in a somewhat arbitrary fashion and persist for only a limited time (one to several years). An appropriate model for describing and predicting population structures in woodland would perhaps contain deterministic aspects, as elaborated by the correlations to abiotic factors (humidity, sodium), as well as stochastic elements, in that the establishment of an aggregation of single populations might occur also more or less arbitrarily. Dominant species often show little evidence of trophic specialization in the field (EVISON 1981). Determinations of transient times of aggregations would be most important for a model of microarthropod communities in the mixed deciduous forest.

The following are still open questions:

Do single aggregations show diffusional outspread? What is the velocity of this outspread and is it an important aspect of colonizing "empty" areas in the soil system? (Some studies on this topic with non-forest microarthropods have been carried out by STREIT & ROSER-HOSCH 1982). What are critical densities, which still allow successful reproduction, and what densities are too low? These problems are especially prominent for the great number of "rare" species in the soil. Do the individual aggregations as demonstrated in this study represent real biological population units with only a minimal gene flow between aggregations (as, e.g., demonstrated to occur in populations of the rather mobile checkerspot butterfly *Euphydryas*, EHRLICH & MURPHY 1981) or does the whole "super population" of the forest form a biological unit, or even a still larger

unit? What are the food preferences of single species that are so dominant at certain sites (e.g. *Oppiella nova* around the beech trunk) and how specialised are these species? Are they opportunistic in what they consume? Studies of this kind are in preparation.

ZUSAMMENFASSUNG

Horizontale Aggregationsmuster und Gradienten in der Populationsdichte bodenbewohnender Milben und Collembolen wurden innerhalb der obersten 5 cm des Bodens eines Laubmischwaldes (*Querco carpinetum* mit eingefügten *Pinus silvestris*) untersucht. Zwischen den einzelnen Baumstämmen wurden teilweise ausgeprägte Dichtegradienten unterschiedlichen Charakters gefunden (Fig. 1 + 2). Innerhalb grösserer Aggregationen von mehreren Metern Durchmesser wurden — v.a. bei den Cryptostigmata — kleinere Aggregationseinheiten gefunden (Fig. 3). Auch andere Strukturmerkmale des Waldbodens, wie Pilze und schwach ausgeprägte Fussgängerpfade (Fig. 4) wurden bezüglich ihrer Auswirkung auf die Populationsdichten untersucht. Wie weit ein korrelativer Zusammenhang zwischen Populationsdichten und messbaren Umweltparametern besteht, wird kritisch diskutiert.

RÉSUMÉ

Les concentrations de microarthropodes (acariens et collemboles) et les gradients de densité de leurs populations ont été étudiés dans une forêt mixte (*Querco carpinetum* avec des pins implantés). D'un arbre à l'autre d'espèces diverses existent des gradients de densités distincts et significativement différents, mais avec chacun son orientation propre pour chaque espèce (Fig. 1, 2). A côté des grandes concentrations (d'un diamètre de plusieurs mètres), il existe de plus petites concentrations (Fig. 3), spécialement chez les oribates. On a d'autre part envisagé l'effet d'autres éléments forestiers, par exemple la présence de champignons ou l'existence de sentiers. On a remarqué que les corrélations entre la densité des microarthropodes et les facteurs écologiques mesurables s'avèrent faibles; cette constatation est particulièrement discutée dans le présent travail. Les facteurs physico-chimiques déterminent peut-être partiellement le développement des associations, qui apparaissent probablement aussi accidentellement, surtout dans le cas apparemment fréquent d'espèces non spécialisées.

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